Quick guide

Spotted hyenas

Kay E. Holekamp

What are spotted hyenas? Spotted hyenas (*Crocuta crocuta*) are gregarious predatory mammals found throughout sub-Saharan Africa. They are the second largest African carnivores after lions, and they are more abundant than any other large carnivore in Africa. They look rather dog-like, yet are more closely related to cats than dogs, and their closest living relatives are the mongooses and civets. Although most people imagine spotted hyenas to be scavengers, they are in fact excellent hunters that feed mainly on large ungulates they kill themselves. An adult spotted hyena can bring down an antelope weighing over three times its own weight, and working together with other hyenas, it can kill ungulates as large as a giraffe or an African Cape buffalo.

Unlike felids, hyenas are endurance hunters: they chase the selected prey animal over long distances until it is winded, and then close in for the kill. Hyenas can be active during the day or night, bear young throughout the year and can survive on a wide array of prey, from termites to elephants. They are keystone predators in many African ecosystems, and their presence is a useful indicator of ecosystem health. Hyenas can survive in environments from which cheetahs, lions and wild dogs have been extirpated; if hyenas also vanish, a particular habitat must have become severely degraded.

Are spotted hyena societies like those of other carnivores? No. Other social carnivores live in small groups in which adults tend to be closely related to each other, and multiple adults often participate in offspring care. Spotted hyenas live in 'clans' containing up to 90 individuals, including multiple unrelated adult males and multiple matrilineal kin groups of related females and their young. The average relatedness among females from different matrilines is very low, and only the mother takes care of its young.

Although hyena clans bear little resemblance to canid packs or lion prides, they are remarkably similar to the societies of old-world primates such as baboons and macaques, particularly in the way they are structured by clear linear dominance hierarchies in which an individual's rank position determines its priority of access to resources. As with female baboons, the social status of a female hyena is determined, not by her size or fighting ability, but by her mother's social rank. In both hyenas and baboons, maternal rank 'inheritance' involves a great deal of social learning that occurs during a protracted juvenile period. The mechanisms by which youngsters acquire their social ranks are the same in hyenas and old-world monkeys. Patterns of competition and cooperation among spotted hyenas are also remarkably like those found in baboons. Although hyenas compete intensively for food, they also rely heavily on cooperative interactions with group-mates to acquire and defend both their social ranks and such key resources as food and territory (Figure 1).

Do these similarities shed light on the evolution of human intelligence? It has long been recognized that humans and other primates have relatively large brains and high intelligence, and two non-exclusive hypotheses have been put forward to account for this. The first suggests that intelligence was favored by environmental factors such as the need to learn when fruit might become available on trees that fruit sporadically, or the benefit of using tools to extract difficult foods. The second, 'social complexity' hypothesis suggests instead that the key selective force was the need to anticipate, respond appropriately to, and even manipulate the labile social behavior of conspecifics. Both hypotheses have received some support, but the strongest evidence is for the social complexity hypothesis.

The social complexity hypothesis predicts that non-primate mammals living in large, intricate societies should exhibit enhanced abilities in the domain of social cognition similar to those found in primates, and show expansion of the frontal cortex areas in the brain known to mediate complex social behavior in mammals. Because the societies of spotted hyena are just as large and complex as those of many primates, they offer an excellent model system in which to test these predictions of the social complexity hypothesis.

Are the social cognitive abilities of spotted hyenas like those of monkeys? Yes: like monkeys, spotted hyenas emit a rich repertoire of visual, acoustic, and olfactory signals which they use to discriminate group mates from alien hyenas, recognize them as individuals and obtain information about their emotional state and circumstances. As in most primates, kin spend much time together and individuals help kin more than non-kin. Even though male hyenas never participate in care of young, spotted hyenas can recognize their paternal as well as maternal kin, as is also true of baboons. Like monkeys, hyenas prefer as social companions individuals who are higher ranking but close to themselves in rank, and subordinate individuals usually initiate these associations; this indicates that hyenas, like many primates, recognize that some group members are more valuable social partners than others. Breeding males prefer to associate and mate with high- over low-ranking females; this is clearly adaptive because cubs of higher-ranking females survive so much better than do those of low-ranking females. Like monkeys, hyenas reconcile after many of their fights, which suggests they need to repair important social relationships that may have been damaged during hostile interactions.

Like monkeys, spotted hyenas can recognize third party relationships based on both social rank and kinship. They can discriminate the ranks of two unrelated group-mates engaged

in a fight, almost always aiding the higher-ranking combatant. They can also recognize the relatives of their former opponents, and after a fight they increase their rates of aggression toward relatives of their opponents, as do old-world primates. Because primates and carnivores last shared a common ancestor 90–100 million years ago, all these similarities in perceptual and social cognitive abilities suggest the action of convergent selection pressure favoring social intelligence in animals confronting the challenges of complex social environments.

Figure 1. Three adult spotted hyenas form an aggressive coalition. (Photo by S.M. Dloniak.)

Are spotted hyenas of interest for traits other than their complex societies? Yes, spotted hyenas exhibit many peculiar traits that set them apart from other mammals and make them uniquely interesting animals. One of the most unusual is the fact that both the behavior and morphology of female spotted hyenas are very heavily 'masculinized'. In contrast to the vast majority of mammals, female spotted hyenas are substantially more aggressive than males and they are socially dominant to males. Females are also about ten percent larger than males. The external genitalia of the female spotted hyena are so similar to those of the male that for centuries people believed these animals were hermaphrodites. The female's clitoris is greatly elongated to form a fully erectile pseudopenis that is virtually indistinguishable from the male's penis, and her vaginal labia are folded together to surround fat and connective tissue, forming a structure that looks very much like the scrotal sac of the male. The female urinates, copulates and gives birth through her pseudopenis. When spotted hyenas mate, the male must insert his erect phallus into the female's flaccid one. During copulation the male squats behind the female and hops around while thrusting blindly upward until he achieves intromission. Inside the female's body, her reproductive tract contains a uterus and ovaries like those of other mammals, but instead of her vaginal canal exiting her body under the tail as occurs in other carnivores, it makes a hairpin turn there and exits the body ventrally through the pseudopenis.

Why did females with such heavily 'masculinized' genitalia evolve in spotted hyenas? No one yet knows the answer to this question, but a number of different hypotheses have been offered as explanations; most of these can be ruled out, but at least two are still in the running. First, if these 'masculinized' genitalia have an adaptive function, they might play an important role in post-copulatory sperm choice for fertilization by female hyenas. Females in the wild often mate with multiple males, and the sperm from these competing males must therefore often occur together in the female's reproductive tract. The ovaries of the female spotted hyena are composed mainly of stromal cells, and contain very little follicular tissue, so the female hyena may have relatively few ova. The female's reproductive tract is long and convoluted, and full of blind alleys and dead ends; perhaps only the highest-quality sperm manage to travel all the way up this strange obstacle course to reach the female's precious eggs.

A second hypothesis is that, instead of having an adaptive function, the female's odd genitalia are merely a side-effect of selection for other male-like traits in females such as large body size or enhanced aggressiveness. If this is true, however, the physiological mechanisms mediating female 'masculinization' on which selection inadvertently acted must have been different from the traditional androgenic mechanisms that sometimes accidentally masculinize chromosomal females in most other species of mammals, including humans. Even when pregnant female spotted hyenas are treated throughout pregnancy with drugs that block the action of androgenic hormones on the fetus, each female offspring of these treated females nevertheless develops a full-size pseudopenis. Furthermore, being born through a long, tube-like phallus is potentially risky for young hyenas as they may sometimes suffocate during parturition, so it seems unlikely that the female's phallus could be adaptively neutral in light of this potential cost.

Where can I find out more about spotted hyenas?

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Department of Zoology, Michigan State University, 203 Natural Sciences, East Lansing, Michigan 48824-1115, USA.
E-mail: holekamp@msu.edu